

Building the climate resilience of arid zone freshwater biota

Final Report

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Published by the National Climate Change Adaptation Research Facility

ISBN: 978-1-925039-82-5

NCCARF Publication 111/13

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Please cite this report as:

Davis, J, Sunnucks, P, Thompson, R, Sim, L, Pavlova, A, Morán-Ordóñez, A, Brim Box, J, McBurnie, G, Pinder, A, Choy, S, McNeil D, Hughes, J, Sheldon, F, Timms, B, 2013, *Building the climate resilience of arid zone freshwater biota*, National Climate Change Adaptation Research Facility, Gold Coast, pp. 30.

Acknowledgement

This work was carried out with financial support from the Australian Government (Department of Climate Change and Energy Efficiency) and the National Water Commission and the National Climate Change Adaptation Research Facility (NCCARF).

The role of NCCARF is to lead the research community in a national interdisciplinary effort to generate the information needed by decision-makers in government, business and in vulnerable sectors and communities to manage the risk of climate change impacts.

The work of Arlene Butwell, Katherine Harrison, Thuy Nguyen on molecular analyses associated with this project is gratefully acknowledged. Sally Hladyz assisted with the production and formatting of the final report. The facilities and support provided to the co-authors by their respective institutions is also gratefully acknowledged. These include: Monash University, Griffith University, University of NSW, Department of Environment and Conservation, WA, Department of Land Resource Management, NT (formerly NRETAS), the Department of Environment and Heritage Protection (formerly DERM) and the Department of Water, SA. This report was developed with financial support from the Australian Government (Department of Climate Change and Energy Efficiency) and the National Climate Change Adaptation Research Facility (NCCARF).

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ABSTRACT

This report describes the research undertaken to develop national guidelines for climate adaptation planning for arid zone aquatic ecosystems and freshwater biodiversity. The guidelines focus on the protection of habitats and processes that support the persistence of freshwater biota under a changing climate. They support policy development, planning and on-ground actions. The major climate adaptation goal is to reduce the risk of the loss of aquatic habitats, deteriorating water quality and the extinction of aquatic and water-dependent species. A portfolio of adaptation approaches to maintaining aquatic habitats, the water resources that support them, and the species that depend upon them, is proposed within a framework of strategic adaptive management. This approach best addresses the uncertainty that exists as to how climatic changes will play out across the arid zone with respect to water availability and ecological processes.

Recommended climate adaptation actions include: combining a national mapping program that identifies the major types of arid zone aquatic ecosystems, their biological assets and the surface water and groundwater resources that sustain them, with vulnerability assessments that determine the climate sensitivity and likely persistence of key habitats; recognising the importance of evolutionary refugia and ecological refuges as priority sites for arid zone climate adaptation planning and policy; protecting a dynamic (spatial and temporal) mosaic of perennial, temporary and ephemeral waterbodies to provide the range of conditions needed to support aquatic and water-dependent species with varying life history traits and dispersal abilities; maintaining the integrity of the dry sediments of temporary and ephemeral waters to ensure the persistence of viable seed and egg banks; recognising the importance of key hydrological and ecological processes, particularly connectivity and dispersal; reducing the existing stressors on aquatic ecosystems and aquatic biota; identifying new and novel waterbodies created by arid zone industries (e.g. mining, pastoralism) that could provide valuable offsets for aquatic systems lost through climatic drying, and implementing climate adaptation actions within a strategic adaptive management framework accompanied by a dedicated program for indigenous, industry and local community engagement and education.

EXECUTIVE SUMMARY

The major goal of climate adaptation for aquatic ecosystems and freshwater biodiversity in the Australian arid zone is to reduce the risk of the loss of aquatic habitats, deteriorating water quality and the extinction of aquatic and water-dependent species. This includes increasing the resilience and, in some cases, the resistance, of the biota of arid zone springs, riverine waterholes, rockholes, lakes and other wetlands to changing water availability, especially increasing water stress. This stress will occur in conjunction with elevated temperatures, an increasing frequency of extreme events and pre-existing environmental impacts, including land degradation and invasive species.

This report describes the research undertaken to develop a portfolio of adaptation approaches to maintaining aquatic habitats, the water resources that support them, and the species dependent upon them, within a framework of strategic adaptive management. This approach best addresses the uncertainty that exists as to how climatic changes will play out with respect to water availability and ecological processes across the arid zone.

Key climate adaptation actions include:

- 1. Identifying key arid zone aquatic assets and assessing vulnerability and risk.**

Spatial information, based on a national mapping program that identifies the major types of arid zone aquatic ecosystems and the surface water and groundwater resources that sustain them, combined with mapping of scenarios of future water availability, is needed to ensure that the locations of vulnerable systems are recognized and the trade-offs between environmental, economic and social water needs and allocations can be accurately assessed. This information will also support development of a national reserve network that adequately represents arid zone wetlands.

- 2. Recognising the importance of evolutionary refugia and ecological refuges as priority sites for arid zone climate adaptation planning and policy**

Evolutionary refugia are freshwater habitats that have supported aquatic species on timescales of millions of years. They are permanent, groundwater-dependent ecosystems (subterranean aquifers, discharge or mound springs and relict streams) that support vicariant relicts (species with ancestral characteristics) and short-range endemics (species that only occur within a very small area). They need to be managed at the aquifer-scale (i.e., the Great Artesian Basin or regional or local aquifers) to ensure that permanent water is maintained. Good water quality and habitat condition needs to be maintained or restored by at individual sites.

Ecological refuges can vary across space and time depending on the dispersal abilities of their biota. The most important are the perennial waterbodies that support obligate aquatic organisms. These species will persist where suitable habitats are available and dispersal pathways are maintained. Protection of the hydrological and aerial connectivity of ecological refuges needs to occur at a whole of landscape scale. Local, site-scale management (including fencing and

eradication of invasive species) is needed to ensure that good quality habitats, fulfilling a variety of refuge functions, are maintained across the arid zone.

3. Protecting a dynamic (spatial and temporal) mosaic of perennial, temporary and ephemeral waterbodies across the arid zone to support the persistence of aquatic and water-dependent species with varying life history traits and dispersal abilities

The presence of waterbodies of varying type, extent and water regime is fundamentally important to the persistence of arid zone aquatic biota. Protecting the integrity of the sediments (dry lake beds) of temporary and ephemeral waters is critical to the persistence of viable seed and egg banks. These, in turn, confer aquatic invertebrate assemblages with resistance and resilience to prolonged drying.

4. Maintaining connectivity and other key processes

This includes identifying and protecting the critical hydrological (groundwater and surface water) processes that support key arid zone waterbodies. Floods are vitally important for maintaining connectivity in dryland river networks. The dispersal of organisms at local, regional and landscape scales is a key ecological process that enables communities to persist across a range of arid zone sites with varying hydrological regimes. Increasing the understanding of how arid zone waterbodies are connected, based on the genetic structure of representative species of fish and aquatic invertebrates, will provide important information for climate adaptation planning, particularly the prioritisation of management and protection efforts. Protecting, restoring and maintaining good quality aquatic habitats is integral to maintaining the key ecological processes that support both fully aquatic and terrestrial water-dependent arid zone biota. Perennial waterbodies provide 'reservoirs' from which species can disperse. Temporary aquatic habitats play important roles as 'stepping stones' between more permanent sites by providing extra resources that enable populations to increase, reproduce and replenish egg and seed banks during wet phases (booms).

5. Vulnerability assessments that determine the climate sensitivity and likely persistence of key habitats

Determining where local climatic processes are decoupled from regional processes provides important information on the likely persistence of aquatic ecosystems under a drying climate. Evolutionary refugia are the most highly decoupled habitats and so will potentially be the most persistent, however, their endemic taxa are the most vulnerable to extinction. Ecological refuges vary in their exposure to climatic influences. Prioritising the protection and management of evolutionary refugia and perennial aquatic ecological refuges is very important because they offer the only chance for in-situ persistence of poorly dispersed species.

6. Reducing existing stressors (particularly the impact of invasive species) on arid zone aquatic ecosystems and freshwater biota

This will increase the resistance and resilience of arid zone biota to changing and increasingly variable climatic conditions and represents an important 'no-regrets' action. Introduced and invasive species (including camels, goats, pigs and donkeys) have been identified as the greatest threat to arid zone

biodiversity. Ongoing support for the Australian Feral Camel Management Program and the creation of additional programs to address the impacts of other feral species and livestock at arid zone waterholes are important climate adaption actions.

7. Identifying new and novel waterbodies created by arid zone industries (e.g. mining, pastoralism) that may provide valuable offsets for aquatic systems lost through climatic drying

The opportunities afforded by creation of new waterbodies by various anthropogenic activities needs to be recognised but the possible trade-offs for biodiversity need to be clearly articulated and rigorously assessed.

8. Implementing climate adaptation actions within a strategic adaptive management framework

Strategic Adaptive Management (SAM) builds upon adaptive management, often defined as ‘learning by doing’, by setting desired future objectives and focusing on integration within social, economic and governance processes. Important elements of SAM for the arid zone include: a coordinated national approach to monitoring and evaluating changes in water quantity and quality in surface and groundwater-dependent ecosystems; inclusion of datasets from environmental impact assessments (EIA) and monitoring and rehabilitation programs undertaken by arid zone industries, including the mining and energy production sector.

9. Engaging indigenous groups, local communities and industry (mining, pastoralism and tourism) with climate change adaptation actions and monitoring

Training and equipment is needed to support the management and monitoring of arid zone aquatic assets and biodiversity by people who live and work in the arid zone. This includes indigenous groups, pastoralists, tourism operators, mining companies and school children. A dedicated program is needed to facilitate community and industry engagement with arid zone climate adaptation actions.

1. OBJECTIVES OF THE RESEARCH

The aim of this research project was to identify the important scales, sites and processes (refugia, connectivity, dispersal, colonisation and establishment) that support the persistence of freshwater biota under a changing climate. This research was undertaken to inform the development of national guidelines for climate change adaptation planning for arid zone aquatic ecosystems and freshwater biodiversity. The guidelines, which are summarised in a separate document, provide a set of climate adaptation actions that are designed to support policy development, planning and on-ground actions. They are designed for use by policy developers, conservation planners, environmental professionals and community members working in natural resource management. These guidelines suggest actions that will help to reduce the risk of the loss of arid zone aquatic habitats, deteriorating water quality and the extinction of aquatic and water-dependent species.

2. RESEARCH ACTIVITIES AND METHODS

Climate change adds an over-arching pressure to freshwater systems already experiencing multiple human impacts. Globally, all freshwater ecosystems are considered vulnerable because of their relative isolation and physical fragmentation within terrestrial landscapes. Arid zone freshwater systems are especially vulnerable because of their extreme isolation by deserts and drylands and very low hydrological connectivity. Increasing demands for water for domestic consumption and food production, and the modification of water regimes and water quality by industry, including mineral and energy extraction processes, represent ongoing impacts. The fundamental drivers of environmental change are an expanding world population and increasing global economic development (Millennium Ecosystem Assessment, 2005). Although there is a trend towards decreasing population densities within the Australian arid zone, the impact of global drivers are still present, as exemplified by expanding resource extraction industries.

2.1 Climate change scenarios

The Australian arid zone faces the scenario of rising temperatures, changing rainfall patterns and amounts, and an increase in extreme events (floods and droughts). Some of the most rapid climate warming recorded since European colonisation of the Australian continent has occurred within the arid zone. Annual maximum temperatures recorded at the Alice Springs meteorological station have increased by 2oC since 1900 while annual rainfall remains highly variable, unpredictable and episodic (Fig. 1). Water availability is the critical factor supporting the persistence not only of freshwater biota but many other arid zone species. We acknowledge that there is some uncertainty as to how climatic changes will play out across the arid zone with respect to water availability. In the southern regions it is likely that annual rainfall will decrease, while an increase may occur in northern regions.

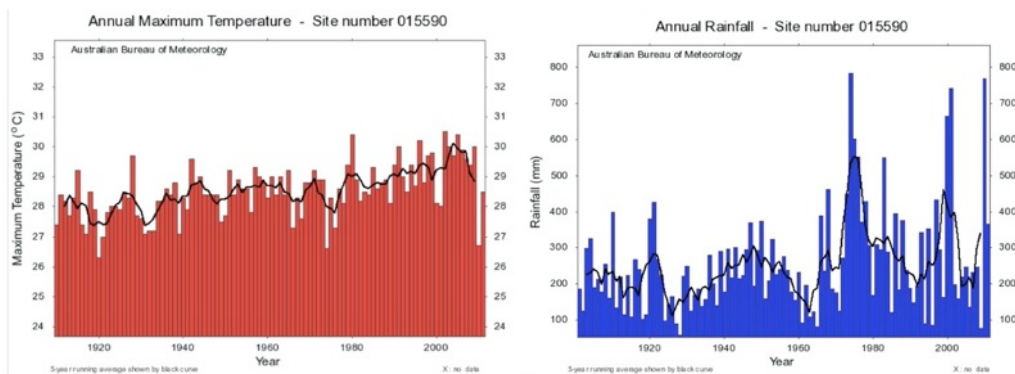


Figure 1. Time series with a five year moving average (continuous line) of: (a) annual maximum temperature; and (b) annual rainfall, Alice Springs, Northern Territory (23.8°S, 133.89°E).

Source: www.bom.gov.au

2.2 Geographical context: the Australian rangelands and the arid biome

The arid and semi-arid regions characterised by low and unpredictable annual precipitation (100-500 mm/year) and extremely high potential evaporation (2880-4000 mm/year) (Fig. 2) make up a distinct biological region, the arid biome. It is the largest biome on the continent, occupying approximately 70% of the landmass (of 7.5 million square kms), and represents one of the largest areas of desert landforms in the world. Arid biomes or drylands cover almost half of the world's land area. The Australian arid zone is a region of low relief (< 300 m above sea level) with the exception of the Pilbara-Hamersley Ranges in Western Australia, the Central Ranges in the Northern Territory and the Flinders Ranges in South Australia.



Figure 2. Extent of arid and semi-arid regions comprising the Australian arid biome Source: Byrne et al. (2008) reprinted with permission, John Wiley & Sons.

Most of Australia's wealth is generated in the arid zone through resource extraction (oil, gas and minerals). Pastoralism is also a major source of economic revenue. Tourism is becoming increasingly important and freshwater ecosystems (springs and waterholes) are often visitor focal points within the arid landscape. Important non-market based aspects of Australian culture are also intrinsic to the region, particularly indigenous culture and the notion of the Outback. The arid biome and the Australian rangelands are largely synonymous. The rangelands support sparsely settled communities comprising 2.3 million people, approximately 13 per cent of Australia's total population. Around 18 per cent of the rangelands are in Aboriginal ownership and management (www.lwa.gov.au).

The rangelands are biologically rich. Over 2,000 types of plants and 605 vertebrate animals have been identified. Further surveys are likely to double the number of plant species. The region contains a significant number of endemic species and habitats for rare, threatened and endangered species. It includes five World Heritage sites and 11 per cent of all listings on the Register of the National Estate. Natural resource management issues, attributable largely to inappropriate land management practices and the presence of introduced species, include: soil salinity; accelerated soil erosion;

increasing numbers and distribution of weeds and feral animals; reduced water quality; altered hydrology; and decreased biodiversity (www.lwa.gov.au).

2.3 Historical context: past climatic changes

The Australian continent has had a long history of climatic change associated with its movement northward since the breakup of Gondwana over 90 million years ago. Aridification appears to have been a feature of the Australian landscape for at least 15 million years. Although Australia did not experience the development of large ice sheets associated with glaciation in the Northern Hemisphere, climatic oscillations did occur. Conditions changed between glacial and interglacial periods from cool and dry to warmer and wetter. Widespread and extreme aridity occurred during the Last Glacial Maximum (LGM), about 18,000 years ago. This extensive history of aridity and fluctuating climatic conditions means that the plants and animals that occur within the arid zone are well adapted to the dry and highly variable climate. The climatic history since European settlement has been one of long droughts interspersed by major floods (Lake, 2011). It is likely that the more frequent occurrence of extreme events will present unprecedented challenges to arid zone biota.

2.4 Determining the major types of arid zone aquatic ecosystems and the water resources that sustain them

Although the arid zone is defined by its low rainfall, a diverse range of aquatic systems occurs within the region. Permanently flowing rivers and deep, freshwater lakes are conspicuously absent (Fig. 3) but permanent, or near-permanent waterholes occur within the extensive dryland river networks. Permanent springs and temporary and ephemeral standing waters of varying area and depth are also present. We sought to develop a simple typology of arid zone waterbodies. This typology, which builds upon the classification of Fensham *et al.* (2011), was based primarily on hydrological (water source) and geomorphological (landform) attributes. We used these attributes because they are relatively fixed, i.e., much less variable than water quantity or quality.

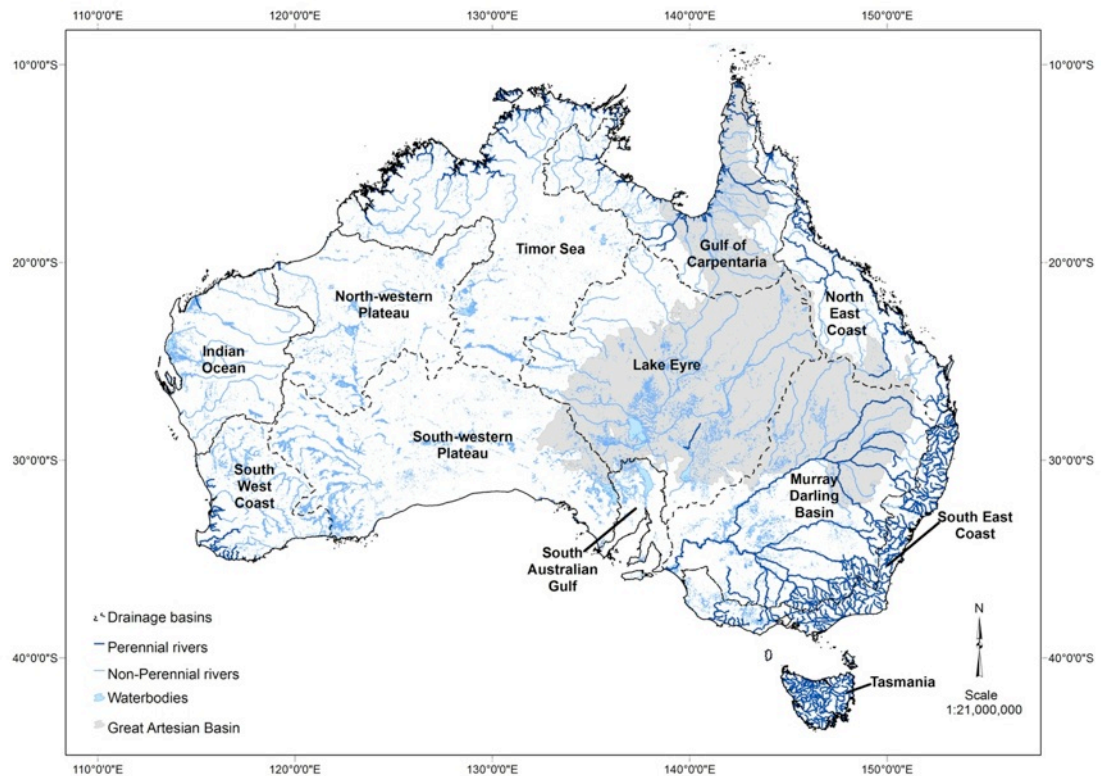


Figure 3. Map showing the location of drainage basins spanning arid and semi-arid zones, watercourses and the Great Artesian Basin Source: GEOFABRIC v.2 surface drainage network layer <http://www.bom.gov.au/water/geofabric>.

2.5 Identifying characteristics of aquatic refugia and likely future persistence

We undertook a review of international and Australian literature to determine the applicability of the concepts of refugia and refuges to freshwater systems in arid Australia. The central role of habitat in the definition of refugia (Keppel et al., 2012) suggests that classifying arid zone aquatic habitats is a useful first step for identifying aquatic refugia. The Australian arid zone contains freshwater ecosystems of varying depths, areas and water quality, surrounded by vast tracts of arid land. Extensive river networks and springs are largely confined to the Lake Eyre Basin (LEB) and the Pilbara-Hamersley region of Western Australia (Fig. 3). Aquatic habitats sustained by groundwater are also present within subterranean aquifers (Humphreys, 2006). Four types of permanent arid zone waterbodies: riverine waterholes, rockholes, discharge springs and outcrop springs, were described for the eastern LEB by Fensham et al., (2011). Riverine waterholes were the most common and widespread while springs and rockholes were confined to relatively discrete clusters. The classification of Fensham et al. (2011) recognised the major geomorphic attributes of these systems, which, being fixed or structural attributes of geology and landform, are much less variable than water quantity or quality. We extended the Fensham et al. (2011) classification across the entire arid zone biome to include subterranean aquifers, relict streams, stream pools, isolated rockholes, claypans and temporary lakes.

2.6 Using molecular genetics to determine population structure, dispersal and genetic connectivity of key arid zone aquatic species

Fieldwork to obtain aquatic invertebrate and fish samples for molecular analyses was undertaken in Central Australia, NT in January 2012 by CI's Davis and Thompson and RA McBurnie (Monash University) and CI Brim Box (NRETAS). Fieldwork to obtain aquatic invertebrate samples for molecular analyses was undertaken in the Pilbara region of WA in June, 2012, by CI Pinder (DEC, WA). Fieldwork to obtain fish samples for molecular analyses in the Western Lake Eyre Basin was undertaken in April-May 2012 by CI McNeil (SARDI, SA).

Mitochondrial COI was used to identify unique lineages in key arid zone aquatic species. Although this marker is relatively conserved, highly transferable across taxa, and has been sequenced for many arid zone aquatic invertebrates, it might not provide enough information on intraspecific variation. To address this, mitochondrial ND5, which is thought to evolve faster than COI, was also used. Although mitochondrial DNA is an excellent phylogeographic tool, it cannot be used as a single genetic marker due to its potential to change differentially with respect to other parts of genome (e.g. if under selection pressure). For this reason, nuclear markers, such as the relatively fast-evolving ITS gene, were also used. Both ITS and COI are suitable for species identification and can reveal the presence of cryptic species. Next Generation Sequencing technology was used to develop species-specific nuclear microsatellite and anonymous nuclear markers for four arid zone species: *Diplacodes haematodes* (dragonfly), *Atalophlebia* (mayfly), Gyrinidae (whirligig beetle) and Turbellaria sp. (flatworm). These markers will be used for coalescent analyses to co-estimate divergence time, effective population sizes and migration rates, as well as for more traditional population genetic analyses. This work is still underway at the time of writing this report. The results will be published as scientific papers and on the web as soon as they become available.

2.7 Determining landscape scale patterns of diversity and distribution of aquatic invertebrate communities across the Australian arid zone using historical data

Historical macroinvertebrate datasets were obtained from previous studies undertaken in the central Australian Ranges, the Pilbara, WA, the Lake Eyre South mound springs, SA, the Diamantina River, Cooper Creek and Coongie Lakes, QLD and isolated rockholes in the Great Victoria Desert, WA (Fig. 4). Multivariate analyses in the Primer software package were undertaken to determine: a) whether there was evidence of biogeographic structuring of communities across the continent; and b) whether different communities were associated with different types of waterbodies. These analyses are in the final stages of completion. The results will be published as scientific papers and on the web as soon as they become available.

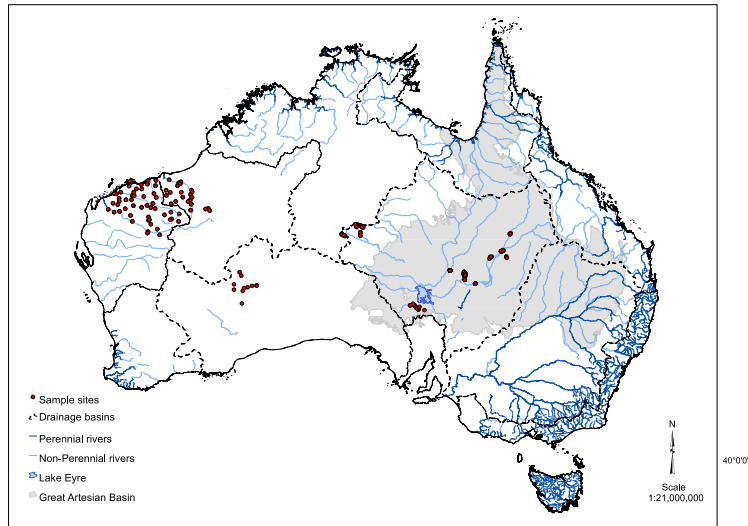


Figure 4. Location of sites from which historical aquatic invertebrate datasets were obtained for this study. Source: GEOFABRIC v.2 surface drainage network layer.

2.8 Climate Change Adaptation Guidelines for Arid Zone Aquatic Ecosystems and Freshwater Biodiversity

A separate document has been written to provide guidance on suitable climate change adaptations for aquatic ecosystems, and the freshwater fauna that they support, across the arid zone. The guidelines have been produced to support policy development, conservation planning and natural resource management (NRM) for a diverse range of aquatic habitats and the freshwater fauna that they support. The guidelines have been produced as a stand alone document, with a minimum of scientific references, to be used by NRM practitioners and other environmental professionals. They are based on the work described in this report and associated scientific papers. A major component of the guidelines is the identification of important types of refugial habitats: evolutionary refugia and ecological refuges. The identification of key refugia was based on an extensive literature review. The result of this review are described in the following sections and are available as an open access paper ([Global Change Biology \(2013\), doi: 10.1111/gcb.12203](https://doi.org/10.1111/gcb.12203)).

3. RESULTS AND OUTPUTS

3.1 The major types of arid zone aquatic ecosystems and the water resources that sustain them

The Australian arid zone contains freshwater ecosystems of varying depths, areas and water quality, surrounded by vast tracts of arid land. Extensive river networks and springs are largely confined to the Lake Eyre Basin (LEB) and the Pilbara-Hamersley region of Western Australia (Fig. 3). Aquatic habitats sustained by groundwater are also present within subterranean aquifers (Humphreys, 2006). The main characteristics of the major systems are summarised as follows.

3.1.1 Subterranean aquifers

Groundwater calcrete aquifers are the most widespread of subterranean aquatic habitats occurring mainly through the central region of WA. The calcretes are discrete, shallow and thin (10–20 m thick) carbonates deposited from the groundwater flow in palaeovalleys immediately upstream of salt lakes. Voids in fractured rock aquifers in the Pilbara-Hamersley region also support aquatic organisms (stygo fauna) (Humphreys, 2006). Arid land subterranean aquatic habitats have greater hydrological stability than do surface water habitats. They are characterised by a lack of light, and associated lack of primary production, and often exhibit marked gradients in organic carbon, oxygen, salinity, redox, pH and water chemistry along groundwater flowpaths and at depths within the aquifer (Humphreys, 2006).

3.1.2 Discharge springs

These are surface expressions of a major regional aquifer, the Great Artesian Basin (GAB), which covers 22% of the Australian continent and is one of the world's largest artesian systems (Prescott & Habermehl, 2008) (Fig. 5). The springs arise through fault structures, where the aquifer adjoins protrusions of basement rock, or where the confining beds are sufficiently thin to allow discharge. Often the springs, also known as mound springs, sustain small permanent downstream wetlands (Fensham et al., 2011). Discharge springs arise in areas remote from where the aquifer receives its input, mainly on the GAB margins (Fig. 3). Long groundwater residence times result in consistent flows and alkaline waters with high concentrations of dissolved solids (Fensham et al., 2011).

Both discharge and outcrop springs (described below) are clustered at a range of scales, from individual vents to spring complexes to 'super-groups' at regional scales. The 'spring complex' scale is defined as a group of springs where no adjacent pair of springs is more than 6 km apart and all springs within the complex are in a similar geomorphic setting (Fensham et al., 2011). Thirteen major super-groups of spatially clustered spring complexes are recognised (Ponder, 2002) (Fig. 5). They represent naturally highly fragmented ecosystems where the springs form aquatic "islands" of biodiversity in a "sea" of inhospitable desert. Floods can result in occasional hydrological connectivity between springs that are located within the same drainage basin.

3.1.3 Outcrop springs

These are habitats that are entirely dependent on groundwater from local aquifers and occur where sediments forming the aquifer outcrop at the surface. The groundwater in these local aquifers can have relatively short residence times and some springs contract to seepages or disappear completely in very dry times (Brim Box et al., 2008). The water is slightly acidic (comparable to rainwater) with low concentrations of dissolved solids (Fensham et al., 2011). The majority of springs in central Australia

discharge from fractured rock aquifers of sandstone, fissured limestone or quartzite, and are usually located near the base of ranges.

3.1.4 Relict streams

These are small, permanently flowing sections of streams in the headwaters of the now mainly dry river systems of the Central Ranges. Local flows occur due to the presence of springs arising from local fractured rock aquifers. They are relatively cool, mesic-type habitats: most occur within deeply shaded, south-facing gorges (Fig. 5). The spring waters are very fresh (often $<100 \mu\text{S}/\text{cm}$) with stable ionic concentrations because shading lessens the evapoconcentrative effects that predominate in more exposed rockholes and riverine waterholes. The term 'relict stream' was first applied by Davis et al. (1993) in recognition of the populations of stream-dwelling insects with Gondwanan affinities that occur in these habitats but nowhere else in the rarely flowing river networks of the Central Ranges. Although these sites can be initially recognised on the basis of geomorphic features they can only be confirmed by the presence of permanent groundwater and taxa with a requirement for shading and cooler thermal regimes. Surveys based on the presence of specific ferns (Peter Latz, pers comm) and aquatic insects (Coleoptera: Psephenidae) have identified eight relict stream sites within the Central Ranges (Davis 1997).

3.1.5 Riverine waterholes

These are the largest and deepest waterbodies that occur throughout the once extensive but now dry river networks of the Australian arid zone. They are connected when large, infrequent rain events result in high flows or flooding (Fig. 3). Between flows they become disconnected and contract in area and depth. Surface water inputs and evaporative processes dominate, although some are sustained by local groundwater inflows (Hatton & Evans, 1998). Riverine waterholes can range from deep, permanent pools to shallow and temporary or very ephemeral pools. They range from 50 m to 20 km in length, with depths > 4 m needed to maintain permanent water (Costelloe et al., 2007, Fensham et al., 2011). Riverine waterholes in the eastern LEB are often turbid (Bunn et al., 2006) while those in the western LEB and Pilbara region are often clear, although smaller creeks can contain highly turbid pools (Pinder et al., 2010).

3.1.6 Stream pools

Episodic rainfall events flood small, rocky headwater creeks in arid zone ranges to create pools (also known as rockholes). Although most are temporary, some exist as permanent or near-permanent pools. They differ from relict streams and outcrop springs in that they are dominated by surface water. They differ geomorphically from riverine waterholes; stream pools occur within first and second order river networks whilst riverine waterholes are located in higher order network sections. Rainfall-induced flow events support short-lived hydrological connectivity along streamlines.

3.1.7 Isolated rockholes

These are natural hollows, formed by fracturing and weathering of rocky landscapes, which store water from infrequent local runoff (Bayly, 2001, Fensham et al., 2011). These are surface water-dominated rather than groundwater-dependent systems. They are the smallest and most isolated of arid zone waterbodies, they are widespread, although not abundant, throughout the region. The pools on granite outcrops in WA represent a subset of this category.

3.1.8 Claypans

These are small, temporary, shallow basins fed by local run off and dominated by evaporative processes. They contain fresh and characteristically turbid water.

3.1.9 Lakes

These are large, shallow, isolated basins with highly variable (temporary to ephemeral) and unpredictable hydroperiods. They are fed by local runoff after infrequent rain events. Extensively vegetated lake systems are often called swamps or marshes.

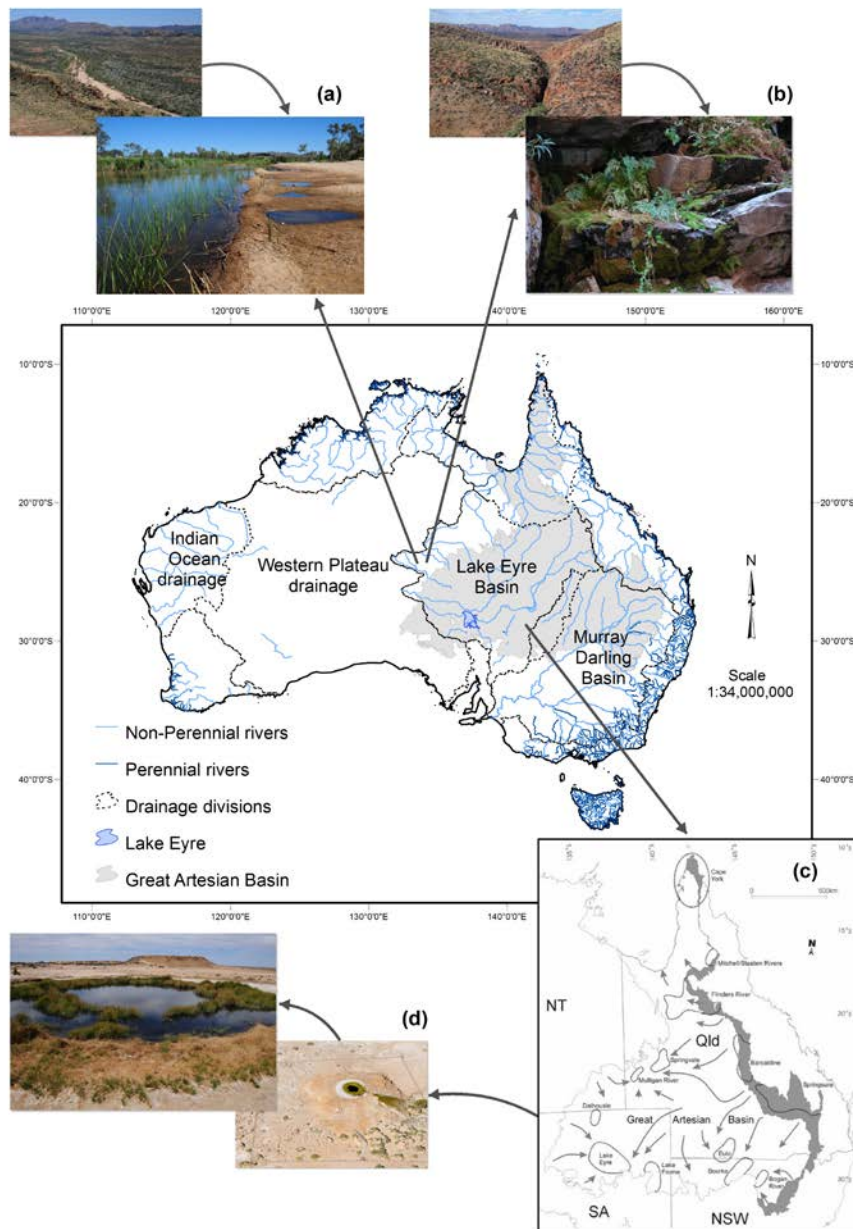


Figure 5. Location of Australia's major river systems and the major arid zone drainage basins: the Lake Eyre Basin, the Murray-Darling Basin (part); the Western Plateau and the Indian Ocean drainage divisions. (a) aerial and ground view of an ecological refuge, Two Mile Waterhole, the Finke River, West MacDonnell Ranges, Northern Territory (23.40 S, 132.40 E); (b) aerial and ground view of an evolutionary refugium, Serpentine Gorge, West MacDonnell Ranges, Northern Territory (23.45S, 132.36E), (c) the Great Artesian Basin showing recharge zones (shaded), spring supergroups (dotted lines), and flow direction (arrows); (d) aerial and ground view of an evolutionary refugium, The Bubbler, a discharge spring in the Lake Eyre South group, South Australia (29.45S, 136.87E). Sources: Base map-GEOFABRIC v.2 surface drainage network layer, Qld map-<http://wetlandinfo.derm.qld.gov.au>, Photos, Jenny Davis.

3.2 The characteristics of aquatic refugia

The central role of habitat in the definition of refugia (Keppel et al., 2012) suggests that classifying arid zone aquatic habitats is a useful first step for identifying aquatic refugia.

We assessed the likely role of arid zone aquatic habitats as evolutionary refugia (based on millennial timescales) by firstly considering the phylogeny (evolutionary history), particularly the time of divergence, of dominant faunal groups (Table 1). Highly divergent lineages are considered to provide evidence of long-term isolation and persistence (Byrne et al., 2008). Refugia can also be identified by the presence of relict species (taxa possessing ancestral characteristics) and short-range endemics (SRE's) sensu Harvey (2002), taxa with highly restricted distributions that occupy a very small area. These include taxa that were formerly more widespread but now occupy much smaller areas and others that are restricted to specific habitats. Important life history traits of SRE's include poor powers of dispersal, confinement to discontinuous or rare habitats, slow growth and low fecundity (Harvey et al., 2011).

Table 1. Attributes supporting the determination of arid zone evolutionary refugia.

Aquatic Habitat	Divergence Time of Dominant Fauna	Short Range Endemics Present	Relictual Species Present	Sources	Likely Importance as Evolutionary Refugia
Subterranean Aquifers	Mid Miocene 3-11 mya	Yes	Yes	1-5	High
Discharge Springs (GAB)	2.5- 0.4 mya	Yes	Yes	6-8	High
Outcrop Springs	Unknown	NR	NR		Low
Relict Streams	Last Glacial Maximum	Yes	Yes	9	High
Riverine Waterholes	2.5 mya - present ~ varying times for different taxa (Mollusca, Crustacea and fishes)	Regional endemism detected in some fish taxa	No	1,10-16	Moderate for permanent & low for temporary waterholes
Stream Pools	Unknown	NR	NR	9	Low
Isolated Rockholes	Unknown	NR	NR	17	Low
Claypans	Unknown	NR	NR		Low
Temporary Lakes	Unknown	NR	NR		Low

NR = Not Recorded.

Sources: (1) Byrne *et al.* (2008), (2) Leys *et al.* (2003), (3) Cooper *et al.* (2007, 2008), (4) Humphreys (2006), (5) Guzik *et al.* (2010), (6) Perez *et al.* 2005, (7) Murphy *et al.*, (2009, 2012), (8) Worthington Wilmer *et al.* (2008), (9) Davis *et al.* (1993), (10) Austin

& Murphy, 2004, (11) Carini & Hughes (2004, 2006), (12) Hughes et al. (2004), (13) Hughes & Hillyer (2003, 2006), (14) Nguyen et al. (2004), (15) Bostock et al. (2006), (16), Unmack (2001a), (17) Bayly (2001).

Subterranean aquifers contain communities of obligate groundwater taxa that represent genetic diversity isolated underground during different geological periods (Guzik et al., 2010, Humphreys, 2006). Crustacean lineages persisting since the breakup of Gondwana include the phreatoicidean and tainisopidean isopods, crangonyctoid amphipods and candonine ostracods. The bathynellaceans (Crustacea) are considered to have persisted since Pangaea. Dytiscid diving beetles and oniscidean isopods are believed to have invaded inland groundwaters during the Tertiary (Humphreys, 2006).

Population genetic analyses of the subterranean dytiscids, *Paroster macrosturtensis*, *P. mesosturtensis* and *P. microsturtensis* provide evidence for multiple expansion events within each species (Guzik et al. 2009). A subsequent comparative study of the genetic diversity and population genetic structure of these dytiscid beetle species, one chiltoniid amphipod species and a lineage of Haloniscus isopods by Guzik et al. (2011) revealed a shared evolutionary history among these subterranean species. They considered it likely that multiple isolation and expansion events had occurred at different times within the study aquifer. The presence of phyletic relictual species, as well as higher taxa typically comprising SRE species, and evidence of population expansion and contraction, suggest that the subterranean aquatic habitat can be classified as an evolutionary refugium.

The evolutionary importance of discharge springs (mound springs) is well documented. The springs support endemic and relict species, dominated by hydrobiid molluscs and crustaceans (including isopods, amphipods and ostracods), with limited mobility and dispersal potential (Murphy et al., 2009, Murphy et al., 2012, Perez et al., 2005, Ponder, 2003, Worthington Wilmer et al., 2008). A molecular study of hydrobiid snails found that at least three separate colonisation events of GAB discharge springs had occurred between 2.5 and 0.4 mya (Perez et al., 2005). Determination of the time-scale of population divergence of the hydrobiid genus *Trochidrobia* found similar results, suggesting that increased periods of aridity and the formation of inland deserts had led to multiple *Trochidrobia* species becoming 'trapped' in desert spring refugia with no subsequent gene flow between populations (Murphy et al., 2012). A phylogeographic study of chiltoniid amphipods found evidence of multiple independent colonisations, particularly within the Lake Eyre group of springs (Murphy et al., 2009). Evidence of a shared evolutionary history between these and WA subterranean amphipods (up to 1500 km away) and approximate dating of the diversity found between major clades suggested that the majority of lineages originated in the late Miocene, coinciding with the onset of aridification. Fish species recorded from the springs represent both endemics of uncertain origin with presumed limited dispersal capacity (Harris, 1992) and widespread species of presumed higher mobility (Wager & Unmack, 2000).

Davis et al. (1993) recognised the evolutionary importance of groundwater-fed, shaded headwater stream habitats in the Central Ranges based on the disjunct distributions of stream-dwelling aquatic insects, including the water penny *Sclerocyphon fuscus*, the mayfly *Atalophebica australis* and the caddisflies, *Hellyethira simplex* and *Ecnomus continentalis*. The low vagility of the adults of these species suggested that they would not be capable of dispersal across the thousands of kilometres of arid land that separate populations in central Australia from the streams where they also occur in southeastern Australia. They suggested that these taxa may have dispersed during a pluvial phase of the Quaternary before the LGM, rather than earlier in the Tertiary,

based on a reconstruction of the phylogeny of the genus *Sclerocyphon* by Davis (1986).

Permanent riverine waterholes act as long-term refuges for fish and fully aquatic invertebrates during dry periods, with long-term population persistence dependent on dispersal and recolonisation among waterholes during periods of high flow (Arthington et al., 2005). Three major types of dispersal strategies have been identified in fragmented dryland river landscapes: 'movers', the organisms that have mobile adults and do not require physical flow connectivity to disperse across waterholes (e.g. Odonata, Heteroptera, Coleoptera); 'networkers', the organisms that disperse easily during the high flow through the channel network (e.g. Crustacea, some fish); and 'permanent refugial' organisms (primarily Mollusca) that have limited dispersal abilities even under flow conditions (Sheldon et al., 2010). The role of riverine waterholes as ecological refuges is well established, but their role as evolutionary refugia needs further investigation.

3.3 Genetic diversity and implied connectivity

Molecular studies have detected significant levels of genetic diversity, both among waterholes within the Lake Eyre and Murray–Darling drainages and between drainages for four species of freshwater mussels, *Velesunio* spp. (Bivalvia: Hyriidae) (Hughes et al., 2004), a freshwater snail, *Notopala sublineata* (Gastropoda: Viviparidae) (Carini & Hughes, 2006), a crayfish, *Cherax destructor* (Decapoda: Parastacidae) (Hughes & Hillyer, 2003), and a freshwater prawn, *Macrobrachium australiense* (Decapoda: Palaemonidae) (Carini & Hughes, 2004). The large scale but infrequent (~10 year) flooding of the 'boom and bust' cycles in the Lake Eyre system (Puckridge et al., 1998) have resulted in less mixing of individuals than would be expected. This is because strong swimmers may actively enter flood currents while weaker swimmers may seek to avoid flood currents and so tend to remain in their waterhole of origin (Hughes & Hillyer, 2006). The importance of these waterholes as evolutionary refugia is likely to be species-specific, indicating the need for more extensive genetic studies to fully determine the extent of isolation of populations of dominant waterhole taxa.

Fishes, which comprise a major component of the biomass of riverine waterholes, are stronger swimmers than most aquatic invertebrates and are known to move out from waterholes onto floodplains during floods (Puckridge et al., 1998). Accordingly, they would be expected to display higher levels of connectivity/gene flow than obligate aquatic invertebrates, but not those with a flying adult phase. Allozyme and mitochondrial DNA data for two species of freshwater fishes, the bony bream *Nematolosa erebi* (Clupeidae) and the Australian smelt *Retropinna semoni* (Retropinnidae) revealed that while there was no contemporary dispersal across the Lake Eyre and Murray–Darling drainage boundaries, there was evidence of historical connections. However, *N. erebi* populations from the two drainages were estimated to have separated c. 150,000 years ago, whereas populations of *R. semoni* were estimated to have separated c. 1.5 million years ago (Hughes & Hillyer, 2006) suggesting different timescales exist for different species with respect to the waterholes acting as refugial habitats.

Further studies of the population genetics of arid zone fishes with different dispersal traits (fast vs. slow dispersers) are currently being conducted to more fully determine the role of riverine waterholes as evolutionary refugia and ecological refuges. For example, Bostock et al. (2006) found very limited genetic diversity within one of the most widespread species, the spangled perch, *Leiopotherapon unicolor*, (Terapontidae) suggesting that it is a very effective disperser, had previously gone through a genetic bottleneck and had probably achieved its current distribution from the

Pleistocene to the present. However, our analysis of this species collected at sites within the eastern Lake Eyre Basin revealed a more complex structure (Fig. 6). This suggests that major barriers to dispersal currently exist and that connectivity within the eastern LEB may not be as great as previously assumed.

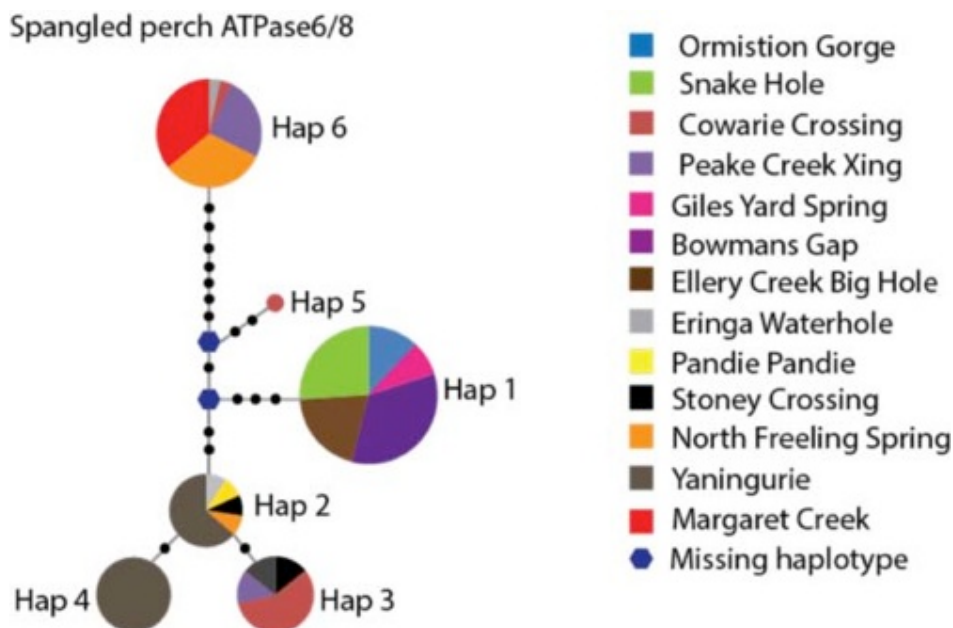


Figure 6. Molecular analysis of a highly dispersive species, the spangled perch, *Leipothorapon unicolor*, sampled at sites in the ephemeral rivers of the eastern Lake Eyre Basin, indicates varying levels of connectivity between waterholes.

3.4 Biogeographic patterns and implied connectivity

Unmack (2001a) investigated the biogeography of the Australian freshwater fish fauna by looking for congruent distributional patterns among species. Connectivity was inferred where species were shared between drainages. Biogeographic patterns were hypothesised and compared with geological and climatic records. Low species richness within some arid regions was attributed to lack of water, and high richness (30 spp) in the Lake Eyre Basin was attributed to its large area and the presence of discharge springs. The high regional endemism found in the Pilbara (42%) and the LEB (40%) were considered to represent divergence arising in the Miocene-Pliocene.

Although a national approach to climate adaptation is important, attention must still be paid to regional and local-scale ecological factors. For example, a comparison of the composition of aquatic invertebrate communities at a range of sites (Fig. 7) across the arid zone revealed a marked dissimilarity between regions.

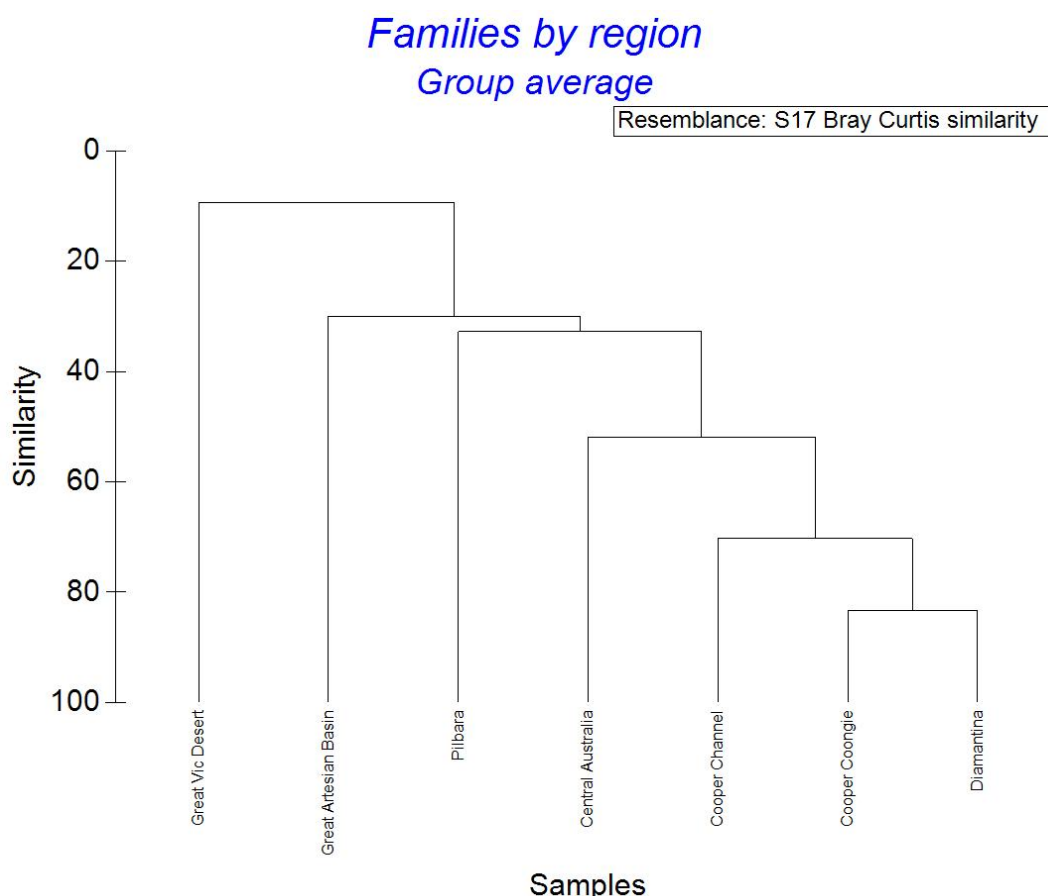


Figure 7. Bray-Curtis similarities of aquatic invertebrate assemblages across the Australian arid zone. Waterbodies contain markedly different assemblages with isolated rockholes in the Great Victoria Desert and mound springs in the Lake Eyre South complex (Great Artesian Basin) being the most dissimilar.

A comparison of the ways in which aquatic invertebrates disperse indicates the importance of aerial dispersal in structuring arid zone invertebrate communities (Fig. 8).

A large component of the invertebrate fauna at all sites (except the isolated rockholes of the Great Victoria Desert) consisted of species that have adult stages that can fly. The dominance of weak flyers (mayflies, caddisflies and small beetles) suggests good dispersal at local and regional scales but not across the entire arid zone (continental scale). The lack of strong active flyers (dragonflies, beetles and waterbugs) in the smallest and most isolated waterbodies (isolated rockholes in the Great Victoria Desert) suggests that large expanses of desert, and the low probability of finding water, act as a barrier to even the most well-adapted arid zone species.

Some aquatic species that cannot fly, in particular, very small crustaceans, are dispersed across dryland regions by wind or by attachment to mobile species such as waterfowl. This is known as passive dispersal. The dominance of passive dispersers in the rockholes of the Great Victoria Desert (GVD) suggests that this is the most important dispersal mechanism for the fauna of this type of habitat. However, the small number of species recorded in the GVD rockholes suggests that this is a relatively inefficient process.

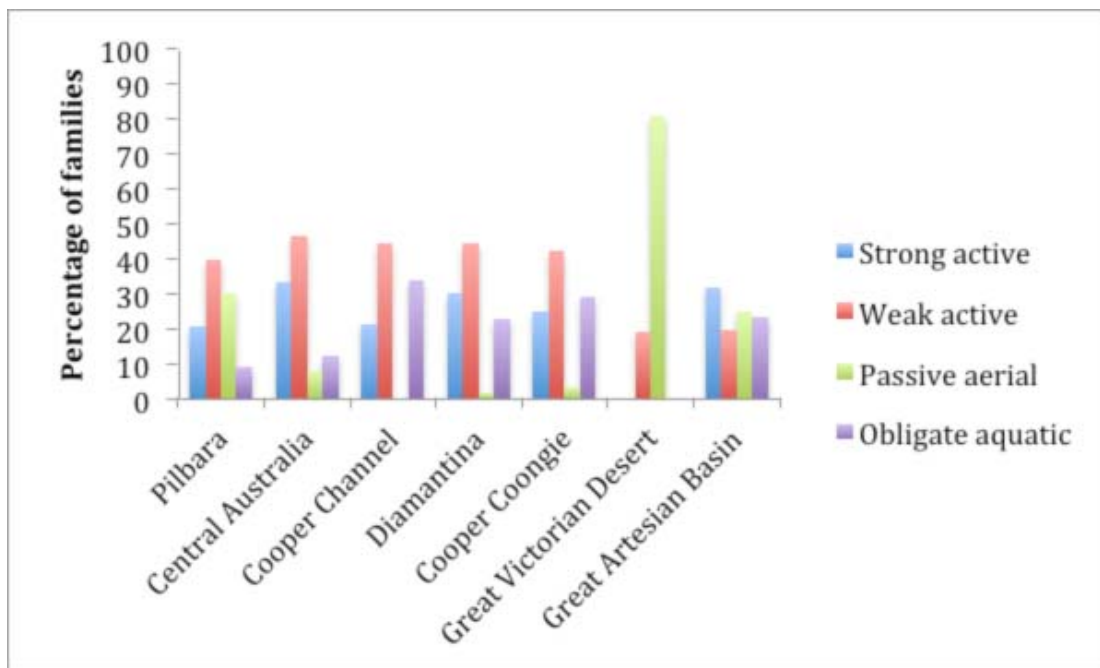


Figure 8. Differences in occurrence of dispersal traits (as percentages of families) of aquatic invertebrates in regions across the Australian arid zone.

Note: this analysis did not include rotifers.

For obligate aquatic organisms (all fish and some aquatic invertebrates, e.g., large crustaceans and molluscs) perennial aquatic systems are the most likely to function as ecological refuges. They are the habitats where aquatic organisms can persist during extended periods without rain. In contrast, the temporary and ephemeral waterbodies that arise as a response to rain events but are short-lived (containing water for only days, weeks or months) are likely to act as refuges for only very mobile taxa (the robust flying adult stages of aquatic insects such as dragonflies and beetles). Some perennial sites can act as both a refugium for species with low dispersal capabilities and a refuge for more mobile species. Perennial waterbodies support meta-population dynamics by providing ‘reservoirs’ from which individuals can disperse. Temporary aquatic habitats play important roles as ‘stepping stones’ between more permanent sites by providing extra resources that enable populations to increase, reproduce and replenish egg and seed banks during wet phases (booms) (Sheldon et al., 2010). Hydrological connectivity is putatively maintained in aquatic habitats located within dryland river networks, but only at the very low occurrence frequencies of large episodic rain events. In contrast, hydrological connectivity is absent (or restricted to very small spatial scales) in isolated standing water and subterranean habitats (Table 2). Accordingly, we hypothesise that the extent of gene flow in species that can disperse only within water (all fishes and some aquatic invertebrates) will be restricted to very small spatial scales in isolated standing-water habitats but extend over much larger, watershed scales in river networks. Gene flow in populations of strong aerial dispersers, such as the Odonata (Aeshnidae, Corduliidae, Gomphidae, Hemicorduliidae and Libellulidae, Coleoptera (Dysticidae, Gyrnidae and Hydrophilidae) and Heteroptera (Notonectidae and Corixidae), will potentially occur at the much larger spatial scales of the entire arid biome or the continent. Gene flow in weaker aerial dispersers, such as Ephemeroptera (Baetidae, Caenidae and Leptophlebiidae) and Trichoptera (Ecnomidae, Leptoceridae and Hydropsychidae), is likely to occur at intermediate (regional) or local scales.

Table 2. Putative hydrological connectivity and scales of gene flow associated with the fauna (fishes and aquatic invertebrates) of arid zone aquatic habitats.

Aquatic Habitat	Type of Refugium/ Refuge	Putative Hydrological Connectivity	Putative Scale of Gene Flow <i>Aquatic Dispersers</i>	Putative Scale of Gene Flow <i>Aerial Dispersers</i>
Subterranean Aquifers	Evolutionary	Low	Local	NA
Discharge Springs (GAB)	Evolutionary & Ecological	Low	Local	Biome
Outcrop Springs	Ecological & Ecological	Low	Local	Biome
Relict Streams	Evolutionary & Ecological	Moderate	Local	Regional
Riverine Waterholes	Evolutionary & Ecological	High	Watershed/ Drainage Basin	Drainage Basin/Biome
Stream Pools	Taxa and context dependent	High	Watershed	Biome
Isolated Rockholes	Taxa and context dependent	None	None	Biome/Continent
Claypans	Taxa and context dependent	None	None	Biome/Continent
Temporary Lakes	Taxa and context dependent	None	None	Biome/Continent

3.5 Likely future refugia

To determine the likely persistence of refugia and refuges in the face of anthropogenic climate change, we examined the environmental processes supporting the formation and maintenance of aquatic habitats with the specific aim of identifying where local processes are decoupled from regional processes, as advocated by Dobrowski (2011) (Table 3). All habitats supported by groundwater are at least partially decoupled from local rainfall. Subterranean aquatic habitats are the most highly decoupled from arid zone precipitation and temperature regimes. Most are supported by groundwater that has accumulated over much longer timescales than that of annual rainfall, and their underground location acts as a buffer from the extreme highs and lows of desert temperatures.

Table 3. Major hydrological and climatic attributes of Australian arid zone aquatic habitats and the likely extent of climatic decoupling.

Aquatic Habitat	Water Source	Hydro-period	Hydrological Variability	Sources	Likely Decoupling from Regional Climate (Rainfall)	Likely Decoupling from Regional Climate (Temp)
Subterranean Aquifers	GW	P	Low	1	High	High
Discharge Springs (GAB)	GW	P	Low	2,3	High	Low
Outcrop Springs	GW	P/I	Low	2,3	Moderate	Low
Relict Streams	GW	P	Moderate	3,4	High	Moderate
Riverine Waterholes	SW/GW	P/I	High	2,3,4, 5,6	Moderate /Low	Low
Stream Pools	SW	I	High	4,6	Low	Low
Isolated Rockholes	SW	I	High	7	Low	Low
Claypans	SW	I	High	8, 9	Low	Low
Temporary Lakes	SW	I	High	8,9	Low	Low

GW = groundwater, SW = surface water, GAB = Great Artesian Basin. P = perennial hydroperiod (permanent aquatic habitat), I = intermittent hydroperiod (temporary or ephemeral aquatic habitat).

Sources: (1) Humphreys (2006), (2) Fensham *et al.* (2011), (3) Brim Box *et al.* (2008), (4) Davis *et al.* (1993), (5) Bunn *et al.* (2006), (6) Unmack (2001b), (7) Bayly (2001), (8) Roshier *et al.* (2001), (9) Boulton & Brock (1999).

The discharge springs, fed by the Great Artesian Basin (a very large aquifer that is mainly recharged from a much wetter climatic zone on the eastern margin of the continent) are the most highly decoupled, spatially and temporally, from annual rainfall (Fig. 5). However, because these springs lack shading by either topographic features or a well-developed canopy of fringing vegetation (as illustrated by the image of a typical representative of a discharge spring in Fig. 5), they are fully exposed to contemporary thermal regimes.

The relict streams present within the Central Ranges, fed by local aquifers, are decoupled from annual rainfall but on shorter timescales (residence time ~100 years) than are the discharge springs supported by the GAB. Their location within shaded gorges also provides decoupling from ambient temperatures (Fig. 5). In contrast, outcrop springs (by definition also supported by local aquifers) are similarly decoupled from annual rainfall, but are not topographically shaded, and so are exposed to ambient temperatures.

Riverine waterholes and stream pools/rockholes are fully exposed to the arid regional climate. Sparse riparian vegetation provides little shelter from the extremes of inland continental temperature regimes (Fig. 5). Large episodic rainfall events are the dominant source of water, resulting in extremely high hydrological variability. Permanent, deep riverine waterholes may also be partially sustained by groundwater held in local aquifers, providing some degree of hydrological buffering under low flow conditions and some thermal buffering, particularly where thermal stratification occurs.

Isolated rockholes, claypans and lakes are usually fully exposed to the regional climate, as they are dependent upon surface water runoff generated by infrequent local precipitation and, unless very deep, are poorly buffered from local temperatures.

4. DISCUSSION

Climate change adaptation is defined as the adjustment of natural or anthropogenic systems to a changing climate for the purpose of moderating impacts or capitalising on novel opportunities (IPCC 2007a). Groves et al. (2012) proposed five approaches to climate change adaptation that can be integrated into existing or new biodiversity conservation plans. These included: (1) conserving the geophysical stage; (2) protecting climatic refugia; (3) enhancing regional connectivity; (4) sustaining ecosystem process and function; and (5) capitalising on opportunities emerging in response to climate change. A major advantage of these approaches is that they are generally robust to the uncertainty in how climate impacts may manifest in any given location.

In this study we have distinguished between aquatic habitats that are likely to act as climatic refugia (evolutionary refugia) because of decoupling from the regional climate (rainfall) and other habitats that will not, but have importance with respect to enhancing regional connectivity and sustaining ecosystem processes and functions.

Mawdsley et al. (2009) proposed 16 adaptation strategies grouped into four broad categories: land and water protection and management; direct species management; monitoring and planning; and law and policy. Although many of these can be considered 'business as usual', these strategies will increasingly need to be viewed through the 'lens of climate-induced changes to species and ecosystems'. For example, the inclusion of evolutionary refugia and major ecological refuges within regional reserve networks represents an important conservation strategy but it will have additional adaptation benefits if the groundwater and surface water resources that support them are also identified and protected. The fundamental importance of groundwater in maintaining evolutionary refugia suggests that mapping and protection of their aquifers is an adaptation action of the highest priority. Important attributes for prioritising the protection of ecological refuges include knowledge of their geographical proximity and degree of connectivity. In the absence of hydrological data, and for spatially isolated waterbodies, this will be provided by obtaining information on the genetic structure of populations of representative species of fish and aquatic invertebrates.

Implementing conservation programs that are good for biodiversity, regardless of future climates, are valuable 'no-regrets' actions (Groves et al., 2012). These include reducing existing stressors such as the over-extraction of aquifers, the impacts of invasive species and habitat degradation. In some cases these impacts may far exceed those of climatic change. Emerging opportunities also need to be considered as part of a broad, strategic approach to climate adaptation planning (Groves et al., 2012). New and novel waterbodies created by arid zone industries (e.g. mining) may represent valuable offsets for ecological refuges lost through climatic drying. These opportunities need to be recognised but the possible trade-offs for biodiversity need to be clearly articulated and rigorously assessed. This is especially important if the creation of new waterbodies has occurred by extracting water from aquifers that support evolutionary refugia.

The establishment of a biome-wide monitoring program, incorporating relatively inexpensive and portable weather stations, aquatic loggers and sampling of key taxa at representative refugial sites is recommended as part of a strategic adaptive management framework. The latter follows a generic process adopted by the IUCN for protected area management based on: setting the 'desired future condition' and management options; operationalisation; and evaluation and learning. This approach

accounts for the complexity arising from interacting drivers that change over time (temperature, rainfall, flow, human skills capacity and levels of trust) and the interdependent behaviours of socio-ecological interactions (Kingsford et al., 2011). It appears well suited to the management of remote arid zone aquatic ecosystems that are located outside protected areas. The data collected will provide feedback on adaptation actions and information on the extent of decoupling of refugial microclimates from larger scale regional climatic change.

Climate change adaptation requires strategies to increase resilience and resistance and to reduce vulnerability, exposure and uncertainty. This applies to species and their habitats, and the processes that support them. Identifying different types of arid zone aquatic habitats as evolutionary refugia or ecological refuges are key concepts that can be used to guide arid zone climate adaptation policy and planning. This classification provides information on the vulnerability of these habitats to a changing climate, particularly a change in water regime, and the processes sustaining community persistence.

Strategies to increase resistance represent a major adaptation goal for arid zone evolutionary refugia where resistance implies the ability to withstand change, despite changing water availability. Evolutionary refugia contain relict and endemic species that have a limited ability to persist in the absence of water, but can display high resistance to changing local conditions. These species are highly vulnerable to local extinctions and must be managed on a site-specific basis. Conservation planning requires a high level of protection for the aquifers that support refugial sites and water quality and habitat conditions must be maintained or restored at individual sites and 'spring-groups'.

Strategies to increase resilience are essential for the conservation of ecological refuges. Here resilience implies that a system or organism will change when water is scarce or disappears, but it will return to the previous state, when water returns. Accordingly, conservation of ecological refuges must focus on supporting dispersal, colonisation and establishment processes, especially maintaining connectivity between waterholes in dryland river networks. This includes ensuring that surface flows are not impounded or diverted, or, if they are, that flows are managed to maintain the spatial and temporal connectivity essential to the persistence of priority aquatic taxa. The importance of floods and variable flow regimes, in maintaining dryland river components and processes, especially fish communities, has been well-documented by Leigh et al. (2010), Medeiros and Arthington (2010), Arthington and Balcombe (2011), Balcombe et al. (2011) and Kerezszy et al. (2011).

Maintaining high quality habitats spanning the distributional ranges of priority taxa, and restoring degraded ecological refuges that are not well represented across the landscape, are also important climate adaptation actions.

Studies that seek to understand multiple, interacting processes (climatic, hydrological, ecological and demogenetic) are needed to further develop strategies to support the persistence of arid zone evolutionary refugia and ecological refuges in an era of unprecedented environmental change. Similar integrative studies which recognise the differences between evolutionary refugia and ecological refuges could also inform the conservation of aquatic and other habitats, and their associated biota, in other biomes.

5. GAPS AND FUTURE RESEARCH DIRECTIONS

The Lake Eyre Basin Knowledge Strategy identified a number of research gaps (<http://www.lebmf.gov.au/publications/pubs/leb-knowledge-strategy-summary.doc>) for arid zone aquatic systems. These include the issue of changes to low-flow hydrology from water abstraction and climate change, the importance of surface water/groundwater exchanges in ephemeral river systems and the effects of tourism and other local scale impacts on waterholes. They identified a need to develop better models and predictions of how changing vegetation cover and condition will affect the quality and quantity of surface run-off and infiltration in arid zone ecosystems. There is also a need to better understand the effects of levees, roads and culvert crossings on downstream flow conveyance and floodplain vegetation. From a social perspective there is a need to better understand the aspirations and values of the broader community and how these may change in the face of a changing climate and economy.

Further molecular studies are needed to determine the present and past connectivity of aquatic sites based on an understanding of the genetic structure of representative aquatic species. This information will also increase the understanding of how important are metapopulation dynamics are in supporting the obligate (fish and aquatic invertebrates) and non-obligate (waterbirds and frogs) communities of arid zone waterbodies.

We have only a limited knowledge of the diversity and ecological roles of algae and aquatic plants in the arid zone. These biota play a major role in arid zone aquatic food webs and are very important in a climate adaptation context.

Relatively little is known about the ecology and biology of stygofauna, in comparison to their diversity, especially in relation to habitat connectivity and environmental water requirements. This is recognised as a knowledge gap in the EIA process for mining in WA by the WA EPA. As a consequence a risk assessment approach is currently being used based on little data.

The flora and fauna of salt lakes is not well documented, despite the ubiquity of salt lakes across the arid zone. Increasing the understanding of the complex playa systems of southern WA is important because these systems are increasingly affected by mining and water disposal. Molecular studies of key species are needed to determine current and past connectivity.

The importance of hyporheic zones as dispersal corridors and ecological refuges and as habitat for future diversification under increasing aridity needs to be determined.

More information is needed on the functional ecology of arid zone wetlands to support the refinement of conceptual models of responses to disturbance. This includes the impacts of altered fire regimes on arid wetlands and the influence of climate change. The effect of livestock on the condition of arid zone wetlands also needs to be determined and addressed.

Research is needed to determine what mix of on-ground management tools is best for building climate resistance and resilience. We need to know when and where reservation, fencing, landscape management, feral animal control and better water resource management can be applied

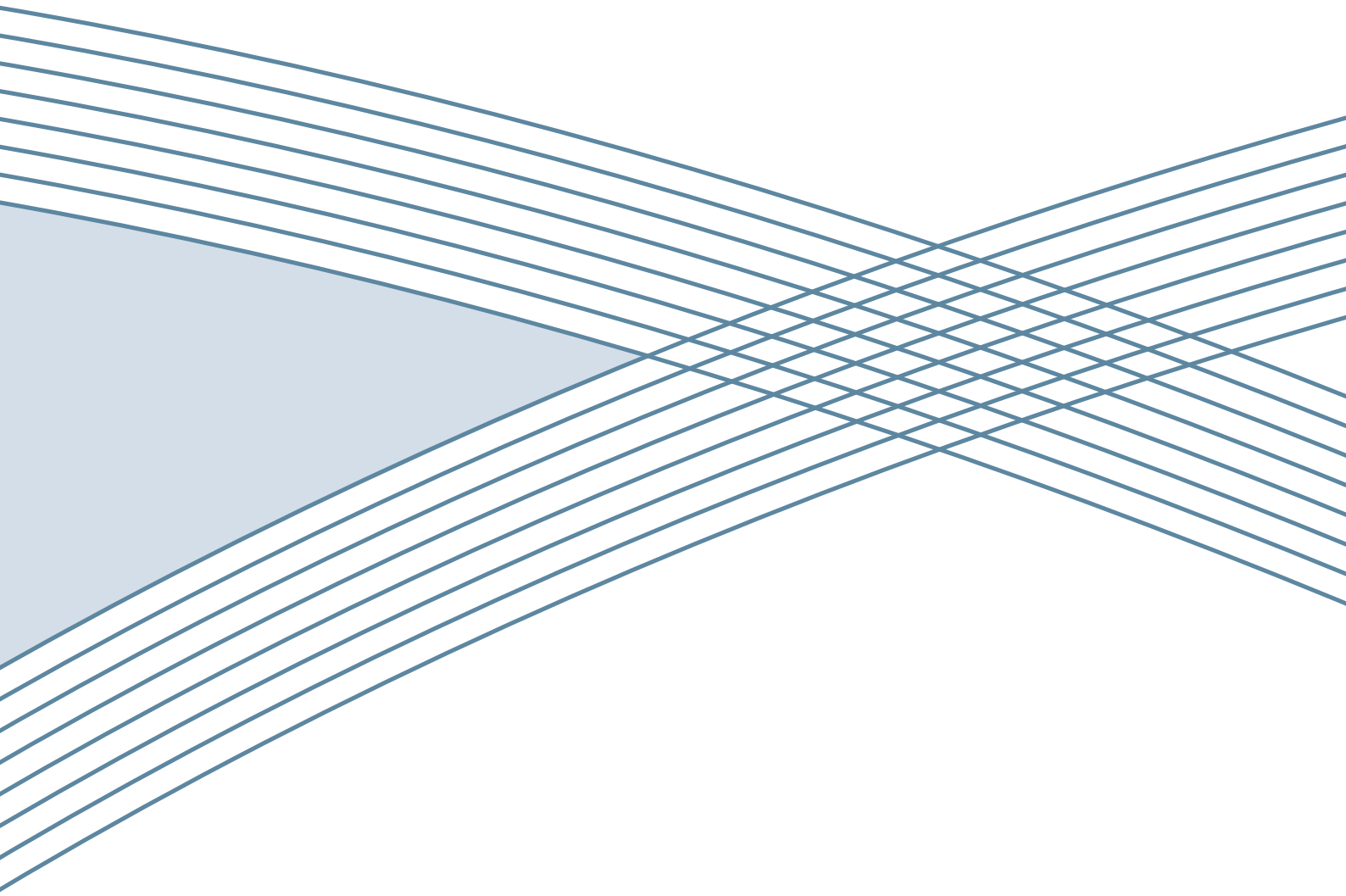
6. REFERENCES

- Arthington AH, Balcombe SR, Wilson GA, Thoms MC, Marshall J (2005) Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. *Marine and Freshwater Research*, **56**, 25-35.
- Arthington AH, Balcombe SR (2011) Extreme hydrologic variability and the boom and bust ecology of fish in arid-zone floodplain rivers: a case study with implications for environmental flows, conservation and management. *Ecohydrology*, **4**, 708–720.
- Austin CM, Murphy, NP (2004) Phylogeography of the widespread Australian freshwater prawn, *Macrobrachium australiense* (Decapoda, Palaemonidae). *Journal of Biogeography*, **31**, 1065–1072.
- Balcombe SR, Arthington AH, Thoms MC, Wilson GG (2011). Fish assemblage patterns across a gradient of flow regulation in an Australian dryland river system. *River Research and Applications*, **27**, 168-183.
- Bayly I (2001) Invertebrate occurrence and succession after episodic flooding of a central Australian rock-hole. *Journal of Royal Society of Western Australia*, **84**, 29-32.
- Bostock B, Adams M, Laurenson L, Austin C (2006) The molecular systematics of *Leiopotherapon unicolor* (Günther, 1859): testing for cryptic speciation in Australia's most widespread freshwater fish. *Biological Journal of the Linnean Society*, **87**, 537-552.
- Boulton, AJ, Brock MA (1999) *Australian Freshwater Ecology: Processes and Management*. Gleneagles Publishing, Adelaide.
- Brim Box J, Duguid A, Read RE, Kimber RG, Knapton A, Davis J, Bowland AE (2008) Central Australian waterbodies: The importance of permanence in a desert landscape. *Journal of Arid Environments*, **72**, 1395-1413.
- Bunn SE, Thoms MC, Hamilton SK, Capon SJ (2006) Flow variability in dryland rivers: boom, bust and the bits in between. *River Research and Applications*, **22**, 179-186.
- Byrne M, Yeates DK, Joseph L et al. (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*, **17**, 4398-4417.
- Carini G, Hughes JM (2004) Population structure of *Macrobrachium australiense* (Decapoda: Palaemonidae) in Western Queensland, Australia: The role of contemporary and historical processes. *Heredity*, **93**, 350-363.
- Carini G, Hughes JM (2006) Subdivided population structure and phylogeography of an endangered freshwater snail, *Notopala sublineata* (Conrad, 1850) (Gastropoda : Viviparidae), in Western Queensland, Australia. *Biological Journal of the Linnean Society*, **88**, 1-16.
- Cooper SJB, Bradbury JH, Saint KM, Leys R, Austin, AD, Humphreys WF (2007) Subterranean archipelago in the Australian arid zone: mitochondrial DNA phylogeography of amphipods from central Western Australia. *Molecular Ecology*, **16**, 1533–1544.
- Cooper SJB, Saint KM, Taiti S, Austin AD, Humphreys WF (2008) Subterranean archipelago: mitochondrial DNA phylogeography of stygobitic isopods (Oniscidea: *Haloniscus*) from the Yilgarn region of Western Australia *Invertebrate Systematics*, **22**, 195–203.

- Costelloe JF, Hudson PJ, Pritchard JC, Puckridge JT, Reid JRW (2007) ARIDFLO Scientific Report: environmental flow requirements of arid zone rivers with particular reference to the Lake Eyre Drainage Basin. In: *Final Report to South Australian Department of Water, Land and Biodiversity Conservation and Commonwealth Department of Environment and Heritage*. Government of South Australia, Department of Water, Land and Biodiversity Conservation.
- Davis J, Harrington S, Friend J (1993) Invertebrate communities of relict streams in the arid zone: the George Gill Range, Central Australia. *Marine and Freshwater Research*, **44**, 483-505.
- Davis JA (1986) Revision of the Australian Psephenidae (Coleoptera): systematics, phylogeny and historical biogeography. *Australian Journal of Zoology*, **119**, (Supplement) 97 pp. CSIRO, Melbourne.
- Davis JA (1997) Conservation of aquatic invertebrate communities in central Australia. *Memoirs of the Museum of Victoria*, **56**, 491-503.
- Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, **17**, 1022-1035.
- Fensham RJ, Silcock JL, Kerecsy A, Ponder W (2011) Four desert waters: Setting arid zone wetland conservation priorities through understanding patterns of endemism. *Biological Conservation*, **144**, 2459-2467.
- Groves CR, Game ET, Anderson MG, Cross M, Enquist C, Ferdana Z, Girvetz E, Gondor A, Hall KR, Higgins J, Marshall R, Popper K, Schill S, Shafer SL (2012) Incorporating climate change into systematic conservation planning *Biodiversity and Conservation* **21**, 1651–1671.
- Guzik MT, Austin AD, Cooper SJB et al. (2010) Is the Australian subterranean fauna uniquely diverse? *Invertebrate Systematics*, **24**, 407-418.
- Guzik MT, Cooper SJB, Humphreys WF, Austin AD (2009) Fine-scale comparative phylogeography of a sympatric sister species triplet of subterranean diving beetles from a single calcrete aquifer in Western Australia. *Molecular Ecology* **18**, 3683-3698.
- Guzik MT, Cooper SJB, Humphreys WF et al. (2011) Evidence for population fragmentation within a subterranean aquatic habitat in the Western Australian desert *Heredity*, **107**, 215–230.
- Harris C (1992) Mound springs: South Australian conservation initiatives. *The Rangeland Journal*, **14**, 157-173.
- Harvey MS (2002) Short-range endemism amongst the Australian fauna: some examples from non-marine environments. *Invertebrate Systematics*, **16**, 555-570.
- Harvey MS, Rix MG, Framenau VW et al. (2011) Protecting the innocent: studying short-range endemic taxa enhances conservation outcomes. *Invertebrate Systematics*, **25**, 1-10.
- Hatton T, Evans R (1998) *Dependence of ecosystems on groundwater and its significance to Australia*, Land and Water Resources Research and Development Corporation, Canberra.
- Hughes J, Baker AM, Bartlett C, Bunn S, Goudkamp K, Somerville J (2004) Past and present patterns of connectivity among populations of four cryptic species of freshwater mussels *Velesunio* spp. (Hyriidae) in central Australia. *Molecular Ecology*, **13**, 3197-3212.

- Hughes J, Hillyer M (2006) Mitochondrial DNA and allozymes reveal high dispersal abilities and historical movement across drainage boundaries in two species of freshwater fishes from inland rivers in Queensland, Australia. *Journal of Fish Biology*, **68**, 270-291.
- Hughes JM, Hillyer MJ (2003) Patterns of connectivity among populations of *Cherax destructor* (Decapoda : Parastacidae) in western Queensland, Australia. *Marine & Freshwater Research*, **54**, 587-596.
- Humphreys WF (2006) Aquifers: the ultimate groundwater-dependent ecosystems. *Australian Journal of Botany*, **54**, 115-132.
- IPCC (2007a) Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Keppel G, Van Niel KP, Wardell-Johnson GW et al. (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, **21**, 393-404.
- Kerezszy A, Balcombe SR, Arthington AH, Bunn SE (2011) Continuous recruitment underpins fish persistence in the arid rivers of far western Queensland, Australia. *Marine and Freshwater Research*, **62**, 1178-1190.
- Kingsford, RT, Biggs HC, Pollard, SR (2011) Strategic Adaptive Management in freshwater protected areas and their rivers. *Biological Conservation*, **144**, 1194-1203.
- Lake, PS (2011) Droughts and aquatic ecosystems: effects and responses. Wiley-Blackwell. Oxford, UK.
- Leigh CF, Sheldon F, Kingsford R, Arthington AH (2010). Sequential floods drive 'booms' and wetland persistence in dryland rivers: a synthesis, *Marine and Freshwater Research* 61: 896–908.
- Leys R, Watts CHS, Cooper SJB, Humphreys WF (2003) Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. *Evolution*, **57**, 2819-2834.
- Mawdsley JR, O'Malley R, Ojima DS (2009) A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conservation Biology*, **23**, 1080–1089.
- Medeiros ESF, Arthington AH (2010) Allochthonous and autochthonous carbon sources for fish in floodplain lagoons of an Australian dryland river. *Environmental Biology of Fishes* **90**, 1–17.
- Millenium Ecosystem Assessment (2005) Ecosystems and Human Wellbeing: Wetlands and Water. World Resources Institute, Washington, DC.
- Murphy NP, Adams M, Austin AD (2009) Independent colonization and extensive cryptic speciation of freshwater amphipods in the isolated groundwater springs of Australia's Great Artesian Basin. *Molecular Ecology*, **18**, 109-122.
- Murphy NP, Breed MF, Guzik MT, Cooper SJB, Austin AD (2012) Trapped in desert springs: phylogeography of Australian desert spring snails. *Journal of Biogeography*. **39**, 1573–1582.
- Nguyen TTT, Austin CM, Meewan MM, Schultz MB, Jerry DR (2004) Phylogeography of the freshwater crayfish *Cherax destructor* Clark (Parastacidae) in inland Australia: historical fragmentation and recent range expansion. *Biological Journal of the Linnean Society*, **83**, 539–5

- Perez KE, Ponder WF, Colgan DJ, Clark SA, Lydeard C (2005) Molecular phylogeny and biogeography of spring-associated hydrobiid snails of the Great Artesian Basin, Australia. *Molecular Phylogenetics and Evolution*, **34**, 545-556.
- Pinder AM, Halse S, Shiel RJ, Mcrae JM (2010) An arid zone awash with diversity: patterns in the distribution of aquatic invertebrates in the Pilbara region of Western Australia. *Records of the Western Australian Museum*, **78**, 205-246.
- Ponder W (2002) Desert springs of the Australian Great Artesian Basin. Conference Proceedings. Spring-fed Wetlands: Important Scientific and Cultural Resources of the Intermountain Region. pp 1-13. Sada, D.W., and Sharpe, S.E. (eds). (2004) Conference Proceedings, Spring-fed Wetlands: Important Scientific and Cultural Resources of the Intermountain Region, May 7-9, 2002, Las Vegas, NV. DHS Publication No. 41210. Retrieved (5/04/13) from Desert Research Institute web site: <http://www.dri.edu>.
- Ponder W (2003) Endemic aquatic macro-invertebrates of artesian springs of the Great Artesian Basin — progress and future directions. *Records of the South Australian Museum Monograph Series*, **7**, 101-110.
- Prescott JR, Habermehl M (2008) Luminescence dating of spring mound deposits in the southwestern Great Artesian Basin, northern South Australia. *Australian Journal of Earth Sciences*, **55**, 167-181.
- Puckridge J, Sheldon F, Walker KF, Boulton A (1998) Flow variability and the ecology of large rivers. *Marine and Freshwater Research*, **49**, 55-72.
- Roshier, DA, Robertson, AI, Kingsford, RT and Green, DG (2001) Continental-scale interactions with temporary resources may explain the paradox of large populations of desert waterbirds in Australia. *Landscape Ecology*, **16**, 547–556.
- Sheldon F, Bunn SE, Hughes JM, Arthington AH, Balcombe SR, Fellows CS (2010) Ecological roles and threats to aquatic refugia in arid landscapes: Dryland river waterholes. *Marine and Freshwater Research*, **61**, 885-895.
- Unmack PJ (2001a) Biogeography of Australian freshwater fishes. *Journal of Biogeography*, **28**, 1053-1089.
- Unmack, PJ (2001b) Fish persistence and fluvial geomorphology in central Australia. *Journal of Arid Environments* **49**, 653-669.
- Wager R, Unmack PJ (2000) Fishes of the Lake Eyre catchment of central Australia. Queensland Department of Primary Industries, Queensland.
- Worthington Wilmer J, Elkin C, Wilcox C, Murray L, Niejalke D, Possingham H (2008) The influence of multiple dispersal mechanisms and landscape structure on population clustering and connectivity in fragmented artesian spring snail populations. *Molecular Ecology*, **17**, 3733-3751.



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